

1 **Interacting with the enemy: indirect effects of personality on conspecific aggression**
2 **in crickets**

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22 **TITLE**

23 Interacting with the enemy: indirect effects of personality on conspecific aggression in
24 crickets

25 **RUNNING TITLE**

26 Indirect effects of personality on aggression

27 **ABSTRACT**

28 In animal contests, individuals respond plastically to the phenotypes of the opponents
29 that they confront. These ‘opponent’ – or ‘indirect’ – effects are often repeatable, e.g.,
30 certain opponents consistently elicit more or less aggressiveness in others.
31 ‘Personality’ (repeatable among-individual variance in behavior) has been proposed as
32 an important source of indirect effects. Here, we repeatedly assayed aggressiveness of
33 wild-caught adult male field crickets *Gryllus campestris* in staged dyadic fights,
34 measuring aggressiveness of both contestants. Measurements of their personality in
35 non-social contexts (activity and exploration behavior) enabled us to ask whether
36 personality caused indirect effects on aggressiveness. Activity, exploration, and
37 aggressiveness were positively associated into a behavioral syndrome eliciting
38 aggressiveness in conspecifics, providing direct evidence for the role of personality in
39 causing indirect effects. Our findings imply that a multivariate view of phenotypes that
40 includes indirect effects greatly improves our ability to understand the ecology and
41 evolution of behavior.

42 **KEY WORDS:** animal personality, behavioral syndrome, aggression, indirect effects,
43 social behavior, crickets

44 INTRODUCTION

45 Over the past decades, research has increasingly focused on the adaptive nature of
46 repeatable among-individual variation in behavior, called ‘animal personality’ in the
47 behavioral ecology literature (Dall et al. 2004; Sih et al. 2004a,b; Réale et al. 2007,
48 2010). This field of evolutionary biology thereby increasingly embraces the notion that
49 natural selection can favor behavioral variation at multiple hierarchical levels, such as
50 within *and* among individuals (Dingemanse et al. 2010b; Araya-Ajoy and Dingemanse
51 2014). While the existence of animal personality is increasingly viewed as representing
52 a ubiquitous feature of natural populations (Bell et al. 2009; Dingemanse et al. 2012b;
53 Garamszegi et al. 2012), recent focus is shifting from questions regarding adaptive
54 causation towards those concerned with the consequences of personality variation for
55 ecological and evolutionary processes (Dall et al. 2012; Wolf and Weissing 2012;
56 Dingemanse and Araya-Ajoy 2015).

57 Social interactions have recently been implicated as an important factor
58 shaping behavioral variation at both the within- and among-individual level
59 (Bergmüller and Taborsky 2010; Montiglio et al. 2013; Dingemanse and Araya-Ajoy
60 2015; Niemelä and Santostefano 2015). Variation within individuals may partly occur
61 because individuals modify their behavior as a function of the phenotypes expressed
62 by conspecifics (so-called ‘indirect effects’; see below). Individuals may alter a
63 particular behavior either in response to the same trait or a different trait expressed by
64 conspecifics. An example of the former effect is provided by reciprocal aggression in

escalating fights, while an example of the latter is provided by aggression in response to opponent body size (Moore et al. 1997).

Indirect effects can have major consequences for ecological and evolutionary processes especially when caused by repeatable differences in phenotypes of social partners that are underpinned by genetic variation. In such cases, the genes of an individual influence the (behavioral) expression of a trait expressed by an interacting individual; such effects are termed 'indirect genetic effects' (IGEs) (Wolf et al. 1998, 1999; McGlothlin et al. 2010). IGEs can greatly influence evolutionary processes particularly when they are correlated with direct genetic effects (DGEs) of an individual's genes on its own phenotype. In mice, for example, aggressiveness is heritable (a DGE), aggressiveness elicited in conspecifics is heritable too (an IGE), and aggressive genotypes elicit greater levels of aggressiveness in conspecifics. Such positive genetic correlations between DGEs and IGEs are predicted to speed up the response to directional selection compared to predictions derived from classic quantitative genetics theory (e.g., McGlothlin et al. 2010). By contrast, negative genetic correlations between DGEs and IGEs might instead impose evolutionary constraints. In gulls, for example, genes expressed in females that contribute to early egg laying (a DGE) actually delay the egg laying date of other females when expressed in their male partners (an IGE) (Brommer and Rattiste 2008). Obviously, phenotypes that are relatively repeatable (e.g., body size) and affect fitness in interaction partners are most likely to induce indirect effects in nature.

86 The consequences of indirect (genetic) effects for evolutionary processes are
87 even more profound when we fully acknowledge the multivariate nature of most
88 phenotypes (Moore et al. 1997; McGlothlin and Brodie 2009; Araya-Ajoy and
89 Dingemanse 2014; Bijma 2014). Behavioral traits are often structured into syndromes
90 (Garamszegi et al. 2012), i.e., whole suites of behaviors are correlated at the among-
91 individual level; such syndromes may impose constraints on micro-evolution of
92 behavior (Dochtermann and Dingemanse 2013). This would, for example, occur when
93 selection favors multivariate behavioral phenotypes that are not present in the
94 population due to strong syndrome structure. To date, studies of syndromes have
95 considered only correlations among ‘direct’ sources of behavioral variation. However,
96 it is likely that indirect effects are also integrated as parts of syndromes. This would
97 occur if, for instance, opponent personality is itself an important source of indirect
98 effects on focal behavior. Indirect effects are expected for behaviors such as
99 aggressiveness and dominance (Moore et al. 1997, 2002), which are themselves often
100 correlated with other behaviors such as boldness, exploration and activity (Garamszegi
101 et al. 2012). Social partner effects should therefore be incorporated as part of
102 behavioral syndromes to better understand the evolution of correlated traits.

103 Aggressiveness represents a good example of an ‘interacting phenotype’
104 studied both in quantitative genetics and behavioral ecology (Wilson et al. 2009; Briffa
105 et al. 2015). Aggressiveness is interesting because of its reciprocal nature and
106 documented occurrence of opponent (also called ‘social partner’) effects (Wilson et al.
107 2009, 2011, 2013; Camerlink et al. 2012, 2013; Alemu et al. 2014). Interestingly,
108 contest theory has traditionally focused on the role of morphological traits such as

109 weapons and body size in shaping the intensity of aggressive interactions (Arnott and
110 Elwood 2008). In empirical studies, however, morphological traits often explain only a
111 moderate portion of the variation in contest behavior (Briffa et al. 2015). The
112 behavioral stress physiology literature implies that behavioral traits may also play an
113 important role because 'proactive' (active, aggressive, explorative, bold) individuals are
114 less responsive to intentions signaled by interaction partners compared to 'reactive'
115 (less active, aggressive, explorative, bold) individuals (Koolhaas et al. 1999; Coppens et
116 al. 2010). While effects of personality on social responsiveness are predicted by game
117 theory (Maynard-Smith 1982; Dall et al. 2004), the idea has received little empirical
118 testing to date (Briffa et al. 2015; Dingemanse and Araya-Ajoy 2015).

119 Crickets are an ideal system to address the occurrence of indirect effects of
120 personality on the expression of aggressiveness. Males of the European field cricket
121 (*Gryllus campestris*) are territorial and frequently engage in agonistic contests to
122 monopolize resources such as burrows or mates (Ritz and Köhler 2007). Wild European
123 field cricket populations show repeatable among-individual differences in suites of
124 traits such as activity, aggressiveness, boldness, and exploratory tendency (Rodríguez-
125 Muñoz et al. 2010; Fisher et al. 2015a,b; Niemelä et al. 2015).

126 Specific study designs are required to quantify variation in individual-level traits
127 where both direct and indirect effects are targeted (Moore et al. 1997; McGlothlin and
128 Brodie 2009; Bijma 2014). We focus here on a design where the same individual has
129 social interactions both as a 'focal' and as an 'opponent', and where each individual
130 plays each role repeatedly across behavioral trials (Wilson et al. 2009, 2013;

Dingemanse and Araya-Ajoy 2015). Such a setup enables the partitioning of the total phenotypic variance in behavior expressed in focal individuals to variance attributable to (i) the focal individual's identity (a direct effect), (ii) the opponent's identity (an indirect effect), and (iii) residual within-individual variance (see Wilson et al. 2009, 2011, 2013 for worked examples). Moreover, because each individual is both used as a focal individual and as an opponent, we can additionally ask whether individuals that (on average) have a high value for a particular behavior also elicit this behavior in conspecifics. Statistically this is measured as the correlation between direct and indirect effects (i.e., the phenotypic components of the genetic correlation between DGEs and IGEs detailed above). Application of this design has, for example, demonstrated that mice with aggressive personalities also elicit aggressiveness in their interaction partners (Wilson et al. 2009). When other traits are additionally measured, their effects may readily be incorporated to ask which (combination of) traits exactly induce social responsiveness in interaction partners (McGlothlin and Brodie 2009; Bijma 2014).

Here, we applied this paradigm to the study of aggressiveness expressed in pairwise interactions. We asked whether the personality of an individual (measured by its average level of activity, exploratory behavior, and aggressiveness across repeated observations) affects the aggressiveness expressed in conspecifics, thus integrating the indirect effects in a multivariate view of the phenotype. We repeatedly assayed activity, exploratory tendency, and aggression to determine the presence of repeatable among-individual variation in these traits ('personality'). To address their indirect effects, we applied a design where each male cricket fought repeatedly in

dyadic interactions, equally often as a focal and as an opponent. We then quantified (i) whether activity, exploratory behavior, and aggressiveness harbored repeatable among-individual variation, (ii) whether individuals were also repeatable in the level of aggressiveness elicited in opponents, (iii) whether an individual's average level of aggressiveness predicted aggressiveness elicited in opponents or (iv) whether other key individual-level characteristics (activity, exploratory tendency, body weight) did so instead. Our second objective was to integrate indirect effects into our description of behavioral syndrome structure. We therefore tested the relative fit of nine alternative hypotheses (models) concerning syndrome structure based on literature, with a structural equation modelling approach (Dochtermann and Jenkins 2007; Dingemanse et al. 2010a); this allowed us to test explicit predictions on the correlation structure among behaviors (detailed in Figure 1). Doing so enabled us to determine the nature of associations between behavioral traits and indirect effects in contest behavior, and thereby forcefully address the consequences of variation in 'personality' during social interactions.

METHODS

Cricket collection

Crickets were collected from a meadow adjacent to the Max Planck Institute for Ornithology (Seewiesen), Germany (47°58'35.5"N 11°14'04.5"E), between the 2nd week of May and the 1st week of June 2013. The main collection site was a south-west facing slope within the meadow. From the 4th week of April onwards, we searched the field

daily for burrows of newly emerged individuals and marked each with a numbered flag. Our aim was to trap individuals close to adulthood because our interest was in quantifying adult behavior (detailed below). We attempted to catch crickets in this stage with funnel traps (detailed in Niemelä et al. 2015) set at the burrow entrance between 10h00-17h00, for up to 30 minutes and up to 4 times per day per burrow, until the individual was caught. We succeeded in catching most crickets within the first two days of attempted catching. Because we monitored burrows on a daily basis, we could track each individual's developmental stage; all captured adults were no more than 1 day post-molting, implying that they lacked experience with mating and fighting. Following capture, crickets were placed in individual containers and transported to a climate room at the Ludwig Maximilians University of Munich. We collected a total of 57 males of which we randomly selected 32 at the onset of the experiments.

Housing

All individuals were housed in a climate room (dimensions: 4.5 l x 3.6 w x 2.7 h m) at 26°C (± 0.5) and 65% (± 0.5) humidity, under a light:dark photoperiod that wild crickets experienced at the time of capture (14:10 h). Each individual was housed alone in a plastic container (10 x 10 x 9 cm) with a sand-covered floor and a flow-through plastic netted lid that prevented escape but allowed air circulation. Each container included an artificial, half-cylindrical shelter (6 x 3.5 x 2 cm), a petri dish (3.5 cm diameter) with food, and another petri dish with water held within a cotton-plugged vial. Individuals

were fed with a mix of dry bird food (Aleckwa Delikat, Germany) and fresh food (carrot and apple) *ad libitum*. Food and water were replaced every 3-4 days. Containers were checked daily for newly molted adults, enabling us to assign age since final molting for each individual not yet molted.

Experimental protocol

Behavioral trials were conducted between the 26th of May and 24th of June 2013. Each individual was repeatedly assayed for each of 3 behaviors (activity, exploration, aggression; described in detail below), on each of 12 consecutive days. Because individual identification is required for the aggression test, subjects were marked with colored tape on the pronotum (red or blue, randomly assigned each time) the day before a trial. The three tests were always done sequentially and in the same order (table 1, figure 2); carry-over effects (from one test on the next) could therefore not be modelled. We chose this set-up because it ensured that all individuals were given the exact same treatment since this greatly facilitates comparison between individuals (Dingemanse et al. 2007; Dochtermann 2010).

We initially selected 32 individuals randomly from the 57 collected individuals. These were divided into eight groups of four individuals according to their estimated age (i.e., days post-molting) to ensure that all the individuals of the same group were approximately the same age. It has been shown that adult crickets within one week post-molting do not show fully developed aggressive behavior (Hofmann and Schildberger 2001); the behavioral assays were therefore conducted when individuals

were at least 7 days post-molting. Groups were on average 9.8 days (standard deviation (SD): 2.6) post-molting at the onset of their behavioral trials. Six individuals died before the end of the experiment and were replaced, increasing the total number of tested individuals to 38. For data analysis (see below), we used all data, including behavioral trials of individuals that died during the experiment and of their replacements.

Within each group of four, each individual was subjected to an aggression test once on each of 12 consecutive days. From previous work, we know that this inter-test interval prevents carry-over effects caused by winner or loser effects (Khazraïe and Campan 1999). To maximize the number of unique pairwise dyads, and sample size per dyad, each individual fought four times with each of the three interaction partners within its group. All individuals within a group of four were tested on the same day, and each of two groups were assayed at the same time (i.e., 8 individuals simultaneously, one group per shelf). To minimize within-group variation in micro-environmental effects, each group was assayed at a fixed time of day over the 12 consecutive days (either between 9h00-12h00, 12h00-15h00 or 15h00-18h00). After each group was tested, walls and dividers of the testing arenas were thoroughly washed with warm water; sand was raked and mixed in a stock container in order to minimize the presence of contact pheromones that could otherwise affect future contests (Judge and Bonanno 2008).

All trials were performed on a rack fitted with two shelves, each equipped with a camera, in the same climate room where the individuals were housed. Arenas were

not acoustically isolated from the rest of the room such that all the individuals were exposed to abundant background noise typical of conditions experienced in the wild. To prevent any visual disturbances, the shelves were isolated from the climate room by white curtains; entrance to the room was not permitted during trials. All trials were recorded using high-resolution digital video cameras (Basler GenICam, Germany) fitted 43 cm above each testing arena. The cameras were connected to a computer outside of the climate room and managed using the software MediaRecorder (Noldus, Netherlands). Videos were recorded at 27.81 frames per second and 1600 x 1200 pixels resolution.

A small number of trials were excluded from the final dataset: 32 of 382 activity and 29 of 382 exploration trials (8.4% and 7.6% respectively) due to technical problems with data recording, and 24 of 191 aggression trials (12.6 %) because males failed to engage in aggressive interactions. Note that the total number of aggression trials is approximately half of that of other trials since two individuals are involved in each aggression test. The final sample size was therefore 350 tests for activity (mean number per individual: 9.2, SD 3.7), 353 for exploration (mean number per individual: 9.3, SD 3.4) and 167 for aggression (mean number per individual: 8.8, SD 3.8).

Behavioral trials and scoring

Activity: The general level of activity in a familiar environment was recorded in the individual's home container. Those home containers were large enough to allow free movement reflecting its routine activity. Prior to the onset of the behavioral trials,

selected individuals were carefully moved to the recording shelves inside their home container and given 30 minutes to acclimatize. To optimize the automated video tracking, the lid, water vial, food and petri dishes were removed from the home containers. Activity was recorded automatically for 60 minutes (Table 1; Figure 2a).

Exploration: Following the activity test, we gently moved the subject (inside its home container) to the side of the shelf where it had previously been filmed, after which we placed two arenas under each camera. These arenas (29.5 l x 15.5 w x 9 h cm) had floors covered with white sand and an opaque removable divider in the middle. When the divider was lowered, the two halves (14.5 l x 15.5 w x 9 h cm) of a single arena could be used as arenas to simultaneously screen, in isolation, exploratory behavior of each of the two individuals that would later meet in an aggression test. At the onset of the exploration test, each individual was moved (inside its own shelter) from its home container to a (randomly allocated) half of the arena. We ensured that all individuals were inside their shelter at the onset of the exploration trial, after which exploratory activity was recorded automatically for 60 minutes (Table 1; Figure 2b).

Activity and exploration videos were analyzed using Ethovision X 10.0 (Noldus, the Netherlands). This software package enables tracking of isolated individuals and extracts the spatial coordinates for each video frame. For both the activity and exploration tests, we used the Pythagorean equation to calculate the distance moved from one frame to the next, using the X and Y coordinates of the individual's center point at each sampling point (User manual of Ethovision X 10.0, Noldus Information Technology 2013). The frame rate at which the videos were analyzed was adequately

set to 6.95 per sec, and we therefore acquired 25020 positions per individual for these 60-min trials. We then summed up all distances to calculate the total distance moved, in the familiar environment (activity test) viewed as a measure of 'activity'. The total distance moved in the novel environment (exploration test) is viewed as a measure of 'exploratory behavior' (following Réale et al. 2007).

Aggression: Following the exploration test, the shelters were removed and the individuals given a further 10 minutes to acclimatize to their half of the arena. The divider was then lifted, after which we filmed each dyad engaging in social interactions for a period of 10 minutes (Table 1, Figure 2c). At the end of each aggression test, each individual was weighed on an electronic balance (precision: 0,001 g). We then changed each individual's color tag according to the next day's schedule, and returned it to the home container in the allotted housing slots within the climate room.

We assayed three behaviors that represented an individual's willingness to engage in aggressive interactions: 'approaching', 'singing', and 'chasing' (defined below). An interaction was defined as starting when any part of one individual touched any part of the other (Bertram et al. 2011), and ended if the contact was interrupted for more than two seconds. Within the 10-minute trial, for each interaction, we scored for each member of the dyad whether it did or did not perform each of these three behaviors. We subsequently counted how often a behavior occurred per individual over the entire trial, resulting in three count variables for each combination of individual and trial. The total number of interactions observed over all 167 trials was 2589 (mean number of interactions per trial = 15.05, min = 1, max = 52). To acquire the

behavioral data, each video was played in slow motion and scored blindly by one of three observers.

Approaching: We scored an individual as 'approaching' during an interaction when it moved towards the other individual from any angle until they came into contact. When only one individual was actively approaching the other (i.e. the other cricket sat still), we assigned the behavior to that individual alone. In cases where both contestants approached each other at the same time, we assigned the behavior to both. The mean number of approaches per individual per trial was 9.64 (min = 0, max = 48). Approach behavior has been used by several studies quantifying aggressiveness in male crickets, sometimes called 'initiating first contact' or 'initiating first aggression' (Brown et al. 2006, 2007).

Singing: Male crickets produce songs by rubbing their wings together when they encounter rivals and this has been reported as an indication of male aggressive intent (Alexander 1961). Singing involves wing movements and is visually easily distinguished from courtship songs and victory songs, the latter produced only by the winner *after* an interaction. The mean number of times singing recorded per individual per trial was 1.73 (min = 0, max = 19).

Chasing: A chase was recorded when one of the contestants (namely, the winner) actively pursued its opponent immediately after the interaction had ended. We defined chases as pursuits in the direction of the loser initiated within 2 seconds after termination of the physical contact. Chasing represents a behavior indicating aggressiveness (i.e. the motivation to continue the fight after contact has ended), and

has also been used as a measure of aggressiveness in several other studies (e.g. Jang et al. 2008; Bertram et al. 2011; Fitzsimmons and Bertram 2013). Unlike the other two behaviors, chasing after an interaction is mutually exclusive for the two individuals, i.e. only the winner ever chases the opponent away. The mean number of chases recorded per individual per trial was 1.46 (min = 0, max = 22).

Statistical analyses

We conducted two sets of statistical analyses. First we partitioned the variation for each measured trait into within- and among-individual variance using a univariate mixed-effect modelling framework. Univariate models allow a straightforward interpretation of fixed effects, and allow for testing repeatabilities of single behaviors. As a second step, we estimated patterns of among-trait covariance at each estimable hierarchical level using a multivariate extension of this framework. All models were fitted using restricted maximum likelihood; dependent variables were mean-centered and variance standardized to facilitate comparison of variance components across traits. Throughout, we assumed a Gaussian error distribution, which was confirmed for all response variables after visual inspection of model residuals.

Univariate mixed-effects models

Sources of variation in traits repeatedly measured in a non-social context (i.e., activity, exploration, and body weight) were estimated by fitting the focal trait as the response variable into a univariate mixed-effect model. To statistically control for potential

sources of variation not relevant to our biological hypotheses we included the following fixed effects: test sequence (covariate, range 0-11), time of the day (minutes from midnight, covariate), shelf (categorical variable with two levels), and location of the arena within a shelf (categorical variable with four levels). Test sequence was coded as the progressive order of repeats for the same assay (0 to 11), such that the fixed effect intercept of the model was estimated for the first test (e.g. Dingemanse et al. 2012a). Time of day was mean-centered, such that the fixed-effect intercept of the model was estimated for the phenotype expressed on the average testing time (following Dingemanse and Dochtermann 2013). We fitted random intercepts for group (8 levels), date (28 levels), and the focal individual's identity (38 levels). Effects of variables fitted to control for variation induced by the experimental design (time of day, shelf, location, group, and date) were unimportant (results not shown) and are not discussed further, except for the variable test sequence which explained significant variation.

Prior to the analysis of the traits repeatedly measured in a social context (i.e., approaching, singing, and chasing), one individual in each trial was randomly assigned the focal and the other the opponent role. Since we hypothesize that focal behavior will depend on opponent phenotype, random intercepts for both focal and opponent identity are included in the univariate model of the focal individual's behavior. Furthermore, because the same individual is the focal in some aggression trials but the opponent in others, the model can be expanded to estimate the covariance (or correlation) between focal and opponent identity effects on focal behaviors. If positive (vs. negative), individuals that are on average aggressive as focal animals also tend to

induce (vs. reduce) aggressiveness in others when acting as the opponent. If opponent identity effects are present but this correlation is zero, individual-level traits of the opponent other than its aggressiveness affect the focal individual's aggressiveness.

While previous studies applying this design have analyzed sources of variation in the focal individual's behavior alone (e.g. Wilson et al. 2009), we were able to record detailed behaviors performed by both individuals in each dyad (i.e. the designation of focal and opponent identities as described above was arbitrary). In order to fully utilize all available behavioral data for parameter estimation we therefore modified the modelling strategy described above as follows. First, we estimated focal and opponent identity effects (as well as their correlation) for the behavior expressed by the focal individual. Second, we structured the dataset in a way that enabled us to simultaneously estimate focal and opponent identity effects (and their correlation) in the behavior of the opponent (as detailed in the Supplementary Text). Third, because focal and opponent roles were randomly assigned, (i) focal identity effects in the focal individual's behavior should equate opponent identity effects in the opponent's behavior, (ii) opponent identity effects in the focal individual's behavior should equate focal identity effects in the opponent's behavior, and (iii) the covariance between focal and opponent identity effects as well as any other fixed-effect (e.g. time of day) and random-effect (e.g. group, date) estimates should be the same for the focal's and opponent's aggressive behavior. We thus implemented a bivariate mixed-effect model with the focal's and opponent's behavior fitted as the two response variables where parameters that were logically identical were constrained to be identical. This bivariate implementation thereby enabled us to utilize all data at hand while simultaneously

avoiding pseudo-replication and biasing effects of arbitrary assignment of focal versus opponent roles. Because of the imposed model constraints, the bivariate model effectively represents a univariate model, and is treated as such in the remaining text.

Adjusted individual repeatability was estimated for each trait by calculating the proportion of the total phenotypic variance not attributable to fixed effects that was explained by individual identity (Nakagawa and Schielzeth 2010). For behaviors expressed in a social context, we additionally calculated the proportion of the total phenotypic variance that was explained by the identity of the opponent and was not attributable to fixed effects, which we call 'adjusted opponent repeatability' (Wilson et al. 2009).

Multivariate mixed-effects models

We estimated patterns of trait covariance at each estimable hierarchical level using a multivariate mixed-effects model. We fitted activity, exploration, and weight as response variables as well as approach as a proxy for aggressiveness. Though we had measured various proxies of aggressiveness (detailed above), we used here only approach because multivariate models including other proxies of aggression did not converge. However, we were able to confirm with sets of simpler models that all proxies for aggressiveness were highly correlated (Results not shown), implying that our decision to use approach as a measure of aggressiveness was justified (for a further discussion on rationale of this approach, see Araya-Ajoy & Dingemanse 2014).

To avoid over-parameterization, we only included fixed (sequence) and random effects (identity of the focal individual) that explained significant variation in the univariate

analyses (see Results). Modelling random intercepts for the focal individual's identity enabled decomposition of phenotypic covariances (and hence correlations derived from them) into among-individual and residual within-individual components (Wilson et al. 2009). Among-individual correlations occur when an individual's average phenotype over all repeated measures is correlated across traits, called a 'behavioral syndrome' in the context of behavior (Dingemanse et al. 2012b); within-individual correlations occur when two phenotypic traits show correlated changes in expression within the same individual due to the combined effects of integration of within-individual plasticity and/or correlated measurement error (Dingemanse and Dochtermann 2013). We further included random intercepts for the opponent's identity for the response variable approach during the aggression test, which enabled us to assess whether individuals were repeatable in the aggressiveness elicited in conspecifics (we will sometimes present this indirect effect as a trait, 'eliciting aggressiveness', for clarity). Because the same individual repeatedly played focal in some and opponent in other trials (see above), we also estimated (i) the correlation between the focal and opponent identity effect on aggressiveness (see above for biological interpretation) as well as (ii) the correlation between the opponent identity effect on aggressiveness and the focal identity effect on each of the other traits (activity, exploration, body weight). This latter type of correlation tests whether individuals that elicit more aggressiveness in others are themselves more (or less) active, explorative, or heavier than individuals eliciting less aggressiveness in others.

Significance testing in mixed-effects models

We tested statistical significance of fixed effects using numerator and denominator degrees of freedom (df) estimated from the algebraic algorithm in ASReml 3.0 (Gilmour et al. 2009). We used likelihood ratio tests (LRTs) to evaluate the statistical significance of random effects. This χ^2 -distributed test statistic is calculated as twice the difference in log-likelihood between a model where a target random effect was fitted versus not fitted (Shaw 1991). Variances are bound to be positive, therefore probability (P) of a LRT applied to a variance was calculated assuming an equal mixture of $P(\chi^2, df=0)$ and $P(\chi^2, df=1)$, i.e. $df=0.5$ (Self and Liang 1987; Pinheiro and Bates 2000; Visscher 2006). Covariances (correlations) are not bound to be positive, and their probability was therefore calculated assuming $P(\chi^2, df=1)$. LRTs involving one variance and one covariance were tested assuming an equal mixture of $P(\chi^2, df=1)$ and $P(\chi^2, df=2)$, i.e. $df=1.5$. We applied this latter test, for example, to evaluate support for opponent identity effects in aggressiveness, which requires fitting both a variance (i.e. the variance attributable to the opponent's identity) and a covariance (i.e. the covariance between focal and opponent identity effects). All models were implemented in ASReml 3.0 (Gilmour et al. 2009).

Structural equation modelling

To test our *a priori* hypotheses on behavioral syndrome structure, we applied structural equation modelling to nine *a priori* conceived scenarios based on the behavioral syndrome literature (described in Figure 1). We analyzed the among-individual correlation matrix estimated from the multivariate mixed-effects model

using the package 'SEM' in the software R v. 3.1.0. (Team R Core 2012). We then statistically compared the models using the Akaike information criterion (AIC) (Akaike 1973; Burnham and Anderson 2002), and evaluated the relative support for each based on AIC differences relative to the model with the lowest AIC (ΔAIC), which represents the best fitting model; we also calculated each model's weight and relative likelihood (Anderson 2008).

RESULTS

Sources of variation in single traits

Exploration, approach, and weight changed significantly within individuals as a function of test sequence (Supplementary Table S1). On average individuals became leaner, less explorative, and less aggressive over the 12-day course of the experiment. None of the traits were significantly affected by tag color, time of day, testing shelf or within-shelf test location (Results not shown); neither did the traits vary between groups or days (Supplementary Table S1).

All traits except singing were significantly repeatable (Table 2); adjusted behavioral repeatabilities were highest for exploration (0.40, SE 0.10) and activity (0.33, SE 0.09), and substantially lower (though significant) for approaching (0.19 SE 0.06) and chasing (0.09 SE 0.05) during the aggression test. Approaching and chasing were significantly affected by the identity of the opponent, though singing was not (Table 2). For approaching and singing, the proportion of variance explained by

opponent identity (i.e. adjusted opponent repeatability) was of a similar magnitude (0.16, 0.06 SE for approaching; 0.12, 0.05 SE for chasing) when compared to adjusted individual repeatability (0.19 and 0.09, respectively). Opponent identity effects imply that unidentified individual-level characteristics of opponents affect the behavior of focal individuals. These effects did not appear to be due to repeatable differences in approaching, chasing or singing among opponents, since the correlation between focal and opponent identity effects was rather weak and non-significant for all three behaviors expressed in the aggression test (Table 2).

Body weight was, as expected also repeatable (Table 1). Interestingly, repeatability was relatively low (0.46, SE 0.11) compared to what might typically be expected. This indicates that body weight strongly depended on day-to-day changes in environmental conditions experienced by our crickets.

Among-trait correlations

Among-individual correlations

The multivariate mixed-effects model provided strong evidence for the existence of among-individual correlations between most traits (Table 3; Supplementary Table S2, Supplementary Table S4). Individuals that were on average relatively aggressive towards conspecifics were also relatively active in a novel environment ('explorative') and relatively active in a familiar environment, providing strong evidence for the

existence of an aggressiveness-activity-exploration syndrome. Furthermore, aggressive individuals were relatively heavy compared to less aggressive individuals.

Our univariate analysis implied that aggressiveness elicited in conspecifics also harbored among-individual variation (Table 2). Aggressiveness elicited in conspecifics was not (tightly) related to an individual's average level of aggressiveness, owing to a non-significant correlation between focal and opponent identity effects (Table 2, see also Table 3). Our multivariate analysis revealed that individuals that were on average relatively explorative in novel environments also elicited approach by opponents in the aggression test (Table 3). This among-individual correlation was relatively strong (0.45, SE 0.17), implying that personality variation with respect to exploratory tendency constitutes a major factor explaining why individuals are repeatable in the level of aggressiveness that they elicit in others.

Residual within-individual correlations

Various traits were also correlated within individuals, implying the existence of integration of within-individual plasticity across multiple traits and/or correlated measurement error. Specifically, when individuals increased their body weight across trials, they also became significantly more explorative in the novel environment (though not more active in familiar environments) (Table 3, Supplementary Table S4). In contrast to patterns observed at the among-individual level, most traits were only weakly and non-significantly associated at the within-individual level.

Behavioral syndrome structure

Based on literature, we constructed and compared nine different *a priori* conceived models of behavioral syndrome structure (Figure 1). The domain-general syndrome, which included correlations between activity, exploration, aggression, and aggression elicited (model 3; Figure 4), best explained the observed data, as inferred from it having the lowest AIC score (Table S3). The second-best model, hypothesizing a domain-general structure with only exploration eliciting aggressiveness (model 9) also had a relatively good fit to the data (model 9: $\Delta AIC=2.35$; Table S3). The domain general model nevertheless fitted the data 3.26 times better compared (Akaike weight of model 3 (0.75) divided by the Akaike weight of model 9 (0.23); Table S3), and is therefore treated as the sole best-fitting model throughout the remaining text.

The four observed behaviors were, notably, also partially independent from each other, as the syndrome structure implied in our best-supported model explained relatively little variation in aggressiveness (Figure 4). Exploration behavior represented an extreme case, where all the among-individual variance was captured by the hypothesized syndrome structure. We verified that this was not an artefact caused by the tight among-individual correlation between exploration and activity, as re-analyses of the data after excluding activity yielded the same results (not shown). These findings therefore provide strong support for the presence of a domain-general syndrome that includes indirect effects.

DISCUSSION

This study investigated the occurrence of indirect effects on aggressiveness in male European field crickets, and asked whether such effects could be driven by personality. As expected, we found evidence for indirect effects as individuals differed consistently in the level of aggressiveness that they elicited in others. Direct and indirect effects on focal behavior were integrated within an overarching behavioral syndrome, existing largely because more explorative individuals were also more active and aggressive, and tended to elicit more aggressiveness in conspecifics. This finding constitutes unambiguous evidence for the notion that an individual's aggressiveness-activity-exploration type influences aggressiveness of conspecifics. Our study thus implies that repeatable differences in behavior represent an important component of the social environment affecting social behaviors of conspecifics. If representing heritable patterns of variation, these findings imply that personality variation in the environment will have consequences for evolutionary trajectories of socially expressed behaviors that would only be appropriately predicted by quantitative genetics theory developed to model indirect genetic effects (Montiglio et al. 2013; Dingemanse and Araya-Ajoy 2015).

Individual and opponent repeatabilities

All behaviors (except singing during the aggression test) were repeatable and their estimates were within the range reported for behavioral traits (meta-analysis: Bell et al. 2009). Values of repeatabilities of non-social behavioral traits (activity, exploration) were also similar to those documented previously in our and other cricket species

(Wilson et al. 2010; Niemelä et al. 2012a,b; Dochtermann and Nelson 2014; Fisher et al. 2015a,b). In contrast, behaviors expressed in a social context (approaching, singing, chasing) had relatively low repeatabilities (0.09-0.19) compared to those expressed in a non-social context (0.33-0.40; Table 2). This was not unexpected since the social environment experienced varied substantially within-individuals across trials, whereas the non-social trials represented a more stable environment. As advocated in recent reviews (Briffa et al. 2015; Dingemanse and Araya-Ajoy 2015), our setup allowed us to assess repeatability of social behavior as it would typically be expressed in the wild (i.e., across an ecologically relevant sample of partners) rather than artificially minimizing social environment effects by using dummies or video playback stimulation. Few other studies of aggression have explicitly modelled such indirect effects by considering identity effects of interaction partners; all such studies have focused on vertebrates. Importantly, the repeatability estimates in these few studies were in the same range of ours (0.11 to 0.27; Wilson et al. 2009, 2011, 2013). These estimates of repeatability are lower compared to the ones reported by meta-analyses (Bell et al. 2009), where aggression was one of the most repeatable classes of behaviors (roughly $R=0.50$). Our findings therefore imply that published estimates might often be substantially biased upwards due to the usage of unnatural standardization standardized experimental conditions (e.g. size matching) that may lack ecological relevance.

Of course, the magnitude of indirect effects that we detected might be less substantial under field conditions. In the wild, other environmental effects (kept stable under laboratory conditions), such as temperature, availability of mates, or predators

might affect the amount of among-individual variation in aggressiveness and aggressiveness elicited in conspecifics. Importantly, studies based on dyadic interactions might typically overestimate the magnitude of IGEs for species that naturally interact in larger groups (Hadfield and Wilson 2007; Bijma 2014). This critic may not be applicable in our case because male-male interactions over ownership of burrows or mates in our study species are typically dyadic under field conditions too (personal observation NJD and FS, Fisher et al. 2016). Therefore, our staged dyadic interactions accurately reflect the natural social environment in which aggressive interactions take place.

The opponent effect provides clear evidence for the notion that individuals plastically adjusted their aggression level in response to the opponent's phenotypic traits that vary at the individual level. Among-individual variation in opponents therefore explains part of the within-individual variation in aggression, which can be interpreted as a social form of phenotypic plasticity, or 'social responsiveness' (Webster and Ward 2011; Taborsky and Oliveira 2012; Wolf and McNamara 2013; Wolf and Krause 2014; Dingemanse and Araya-Ajoy 2015). By modelling the opponent identity as a random effect, we integrated the influence of all the aspects of an opponent's individual-level phenotype. However, by also measuring phenotypic traits of the opponent (including its personality), we were able to tease apart which traits were driving the opponent effect as we describe below.

Individual-level correlations of behavioral traits across contexts

Among-individual correlations between focal aggression, exploration and activity were positive, confirming our predictions and revealing a syndrome structure including behaviors expressed in social and non-social contexts. Positive correlations among activity and exploration behavior are well-documented in the behavioral syndrome literature (Sih et al. 2004b; Réale et al. 2007; Garamszegi et al. 2012), and are generally supported in crickets (e.g. Wilson et al. 2010, but see Dochtermann and Nelson 2014). The coping style literature predicts the presence of bold, exploratory, and aggressive individuals called ‘proactive’ types (Koolhaas et al. 1999; Coppens et al. 2010), which we indeed found in our study. We note however, that the relationship between aggressive behavior and other personality traits is often population-specific (Bell 2005; Dingemanse et al. 2007). Our findings therefore confirm the notion that behaviors from different functional contexts covary and that domain-general syndromes may be common among organisms (Sih et al. 2004a,b; Bell 2007; Dochtermann and Jenkins 2007). Such a structure may be important from an evolutionary perspective because trait correlations are known to affect evolutionary trajectories (Lande and Arnold 1983; Sih et al. 2004b; Sprenger et al. 2012; Dochtermann and Dingemanse 2013).

The repeatable part of an individual’s weight was correlated with an individual’s average level of exploration and aggressive behavior, implying that repeatable variation in body condition might have proximately underpinned the observed behavioral syndrome (see e.g. Royauté et al. 2015b). However, post hoc analyses showed this not to be the case: we conducted a set of SEMs expanding

upon our best-supported (domain-general) model. We then compared the relative fit of models where body weight constituted an additional expression of the latent variable rather than representing the latent variable itself (versus a null model where body weight was not associated with behavior) (Figure S1, Table S5). The domain-general model, where body weight also constituted an expression of the latent variable, was best supported; this finding implies that weight indeed did not ‘drive’ the syndrome structure. Interestingly, body size has often been hypothesized to represent an important mediator of agonistic behavior in the animal contest literature (Briffa et al. 2015). Our study implies that social partners responded to personality rather than other characteristics of conspecifics, such as their body weight. It is of course possible that crickets instead responded to *relative* differences in body weight. However, this scenario is not supported by our data because it should result in effects of the unique combination of focal and partner identity effects (so-called ‘pair identity’ effects), which were not present when modelled in our data (Results not shown).

Because behaviors are plastic, feedbacks between traits may occur during interactions and can either increase or decrease the amount of among-individual variation (Moore et al. 1997; Wolf et al. 1998, 1999; Dingemanse and Araya-Ajoy 2015; Sih et al. 2015). The level of aggression in one individual is often affected by the aggression displayed by the interacting individual in escalated fights (Huntingford and Turner 1987), and positive correlations between the focal and opponent effects on this trait would indicate this type of reciprocal feedback. By contrast, if aggression in part reflects dominance (e.g., with dominant individuals only displaying aggression towards subordinates), negative correlations can arise (Wilson et al. 2011). Interestingly, the

lack of a significant correlation between being aggressive and eliciting aggression in others may suggest the absence of feedback loops (either positive or negative) in this trait. However, our SEM-analysis uncovered a relationship between being aggressive and eliciting aggressiveness underpinned by the behavioral syndrome (see below), indicating that positive feedbacks may have been present instead.

In contrast to patterns found at the among-individual level, most traits were only weakly and non-significantly associated at the within-individual level. This suggests that trait correlations were caused by different proximate mechanisms within versus among individuals (van Noordwijk and de Jong 1986; Hadfield et al. 2007). This finding contrasts recent studies reporting within- and among-individual correlations of similar magnitude (Araya-Ajoy and Dingemanse 2014; Brommer et al. 2014; Royauté et al. 2015a). The partial difference in correlation structure at the within vs. among individual level highlights the importance of separating the two in order to make unbiased inferences about behavioral syndrome structure (Dingemanse et al. 2012b; Dingemanse and Dochtermann 2013; Brommer et al. 2014).

Integration of indirect effects as part of a multivariate behavioral phenotype

All behavioral traits were linked with aggressiveness elicited in conspecifics as part of a behavioral syndrome, highlighting the key importance of considering the opponent's personality in the expression of social behaviors. These findings are supported both by the multivariate mixed-effect model and the SEM. Because exploration, aggression and activity were highly correlated, we expected that they would jointly affect the

aggression of conspecifics, implying that the syndrome as a whole would explain the indirect effects on aggression (model 3). This was indeed the case: despite the ‘penalization’ for a higher number of parameters, the best-supported model was the one with a domain-general behavioral syndrome (Table S3, Figure 4). A mechanism for the overarching indirect effect could be that individuals who explore a new environment are likely to also be involved in more social interactions and this may result in more attacks received by others within an aggression trial. This interpretation is warranted by the strong bivariate correlation between indirect effects on aggression and exploration in the among-individual correlation matrix. Indeed, exploration was the factor loading most strongly with the latent variable in our structural equation model. The overarching importance of exploration behavior was implied by the second-best fitting model, which attracted some support (Table S3). Indeed, movement variables may represent obvious cues of an individual’s aggressiveness. Nevertheless, other components of the behavioral syndrome definitely played an important role in eliciting aggression because a full domain-general model was over three times better supported. Because indirect effects were integrated as part of the behavioral syndrome, our findings imply that studies of the evolution of behavior should explicitly recognize that behavioural phenotypes are multivariate and include responses of the social environment.

Evolutionary implications

Adaptive explanations in the field of behavioral ecology are often based solely on phenotypic observations, with evolutionary inference relying on the ‘phenotypic gambit’, assuming correspondence of phenotypic and genetic patterns of (co)variation (Grafen 1984). Support for this position has been provided by a behavioral meta-analysis in which phenotypic correlations explained 75% of the variation in genetic correlations (Dochtermann 2011), although this correspondence should not readily be assumed for individual cases. Despite this important caveat in our knowledge, the presence of indirect effects documented here suggests a strong potential for IGEs to contribute to evolutionary trajectories of aggression and/or traits genetically correlated with it, which in our case include exploration and activity. Our study thus implies that behavioral types certainly have the potential to alter the evolutionary trajectories of behavioral traits by inducing indirect effects in a social context. Further partitioning the repeatable among individual behavioral variance into additive genetic and environmental effects would enable us to move from studying causes to revealing the consequences of personalities. This would ultimately enable us to predict the evolutionary consequences of the very existence of personality types in natural populations.

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939

FIGURE LEGENDS

Figure 1. Models (1–9) of hypothesized relationships between behaviors (syndrome structure). Unidirectional arrows represent causal relationships between variables, bidirectional arrows represent correlations. Solid lines represent relationships present across the whole set; dashed, dotted, and mixed lines represent relationships expressed in specific syndrome structures. Model 1: null model of behavioral independency (Coleman and Wilson 1998). Model 2: coping styles with ‘proactive’ and ‘reactive’ types (correlations among exploration, activity and aggression) (Koolhaas et al. 1999; Coppens et al. 2010). Model 3: The dashed arrow is active; a modification of model 2, where all behaviors including the indirect effects are expression of a general-domain syndrome. Models 4-6: the dashed arrow alone is active in model 4, the mixed arrow alone in model 5, both in model 6. Semi-independency of modules (Sih et al. 2004b) for different contests (social and non-social behaviors). Model 7: the dashed arrow is active; combination of model 2 with reciprocal feedbacks on aggressiveness (covariance between aggression and eliciting aggressiveness) (Moore et al. 1997; Wilson et al. 2009). Models 8-9: the mixed arrow is active only in model 8, the dotted arrow is active only in model 9; combination of model 2 with ideas from (Verbeek et al. 1996). Exploration, aggression, and activity are part of syndrome and either exploration (8) or activity (9) has a direct effect on aggressiveness of others.

Figure 2. Daily experimental timeline, showing a top view of the experimental setups used to measure a) activity b) exploration and c) aggression.

Figure 3. Graphical illustration of the indirect effect of exploration behavior on aggression. We present here correlations between BLUPs derived from the multivariate mixed-effects model: individual-mean levels of exploration (x axis) and aggression elicited in the opponents (y axis). Each point represents the BLUP of an individual (in standard deviation units) with its associated standard error.

Figure 4. Parameter estimates of the structural equation model that best fitted our data. For each variable, we report the variance explained by the SEM structure (R^2) and factor loadings with the corresponding SE in parentheses. These represent how behavioral responses are predicted to change based on changes to the underlying syndrome structure.

971 **TABLES**

972 **Table 1.** Timetable of the daily experimental procedure (see the Methods for further
973 details). Each individual was subjected to this procedure for 12 consecutive days.

Order within day	Action/behavioral test	Location	Duration
1	Food and water removal + acclimation	Home container	30 min
2	Activity	Home container	1 hr
3	Transfer to exploration arena		1 min
4	Exploration	Exploration arena	1 hr
5	Shelter removal + acclimation	Exploration arena	10 min
6	Aggression	Exploration arena w/o divider	10 min

974 **Table 2.** The proportion of total phenotypic variation not attributable to fixed effects explained by focal identity (adjusted individual
975 repeatability; direct effects) and opponent identity (adjusted opponent repeatability; indirect effects), and the correlation between focal
976 and opponent identity effects. Positive values for this correlation indicate patterns where individuals that on average express a high value
977 for the given behavior also elicit an increased expression of this behavior in opponents. Estimates (with SE) are derived from univariate
978 mixed-effect models with random intercepts for focal and opponent identity as appropriate, and associated χ^2 -values, degrees of
979 freedom (df), and values of P derived from likelihood ratio tests where the full model is compared to one where the random effect of
980 interested was excluded.

Trait	Individual repeatability (SE)	χ^2 df	<i>P</i>	Opponent repeatability (SE)	χ^2 df	<i>P</i>	Focal - opponent correlation (SE)	χ^2 df	<i>P</i>
Activity	0.33 (0.09)	65.60 _{0.5}	<0.01	-	-	-	-	-	-
Exploration	0.40 (0.10)	92.56 _{0.5}	<0.01	-	-	-	-	-	-
Weight	0.46 (0.11)	253.37 _{0.5}	<0.01	-	-	-	-	-	-
Approach	0.19 (0.06)	17.65 _{1.5}	<0.01	0.16 (0.06)	14.74 _{1.5}	<0.01	0.22 (0.26)	0.70 ₁	0.40
Chase	0.09 (0.05)	6.49 _{1.5}	<0.05	0.12 (0.05)	9.72 _{1.5}	<0.05	-0.34 (0.39)	0.71 ₁	0.40
Sing	0.07 (0.05)	3.60 _{1.5}	0.11	0.05 (0.05)	1.86 _{1.5}	0.28	-0.21 (0.56)	0.15 ₁	0.69

982 **Table 3.** Estimated among- and residual within-individual correlations (with associated SE) for two non-social behaviors (activity and
983 exploration), two social behaviors (aggressiveness and aggressiveness elicited in opponents), and weight. We present among-individual
984 correlations on the upper off-diagonals and within-individual correlations on the lower off-diagonals. Correlations printed in bold-face are
985 significant based on likelihood ratio tests derived from the multivariate model detailed in the main text. Note that the experimental setup
986 solely allowed for estimating of among-individual correlations with aggressiveness elicited in other individuals.

	Aggressiveness	Activity	Exploration	Weight	Aggressiveness elicited
Aggressiveness	-	0.39 (0.18)	0.39 (0.17)	0.43 (0.16)	0.09 (0.22)
Activity	-0.02 (0.07)	-	0.81 (0.08)	0.17 (0.15)	0.16 (0.20)
Exploration	0.03 (0.07)	0.17 (0.06)	-	0.22 (0.14)	0.45 (0.17)
Weight	0.05 (0.06)	0.06 (0.06)	0.13 (0.06)	-	-0.31 (0.18)

FIGURES

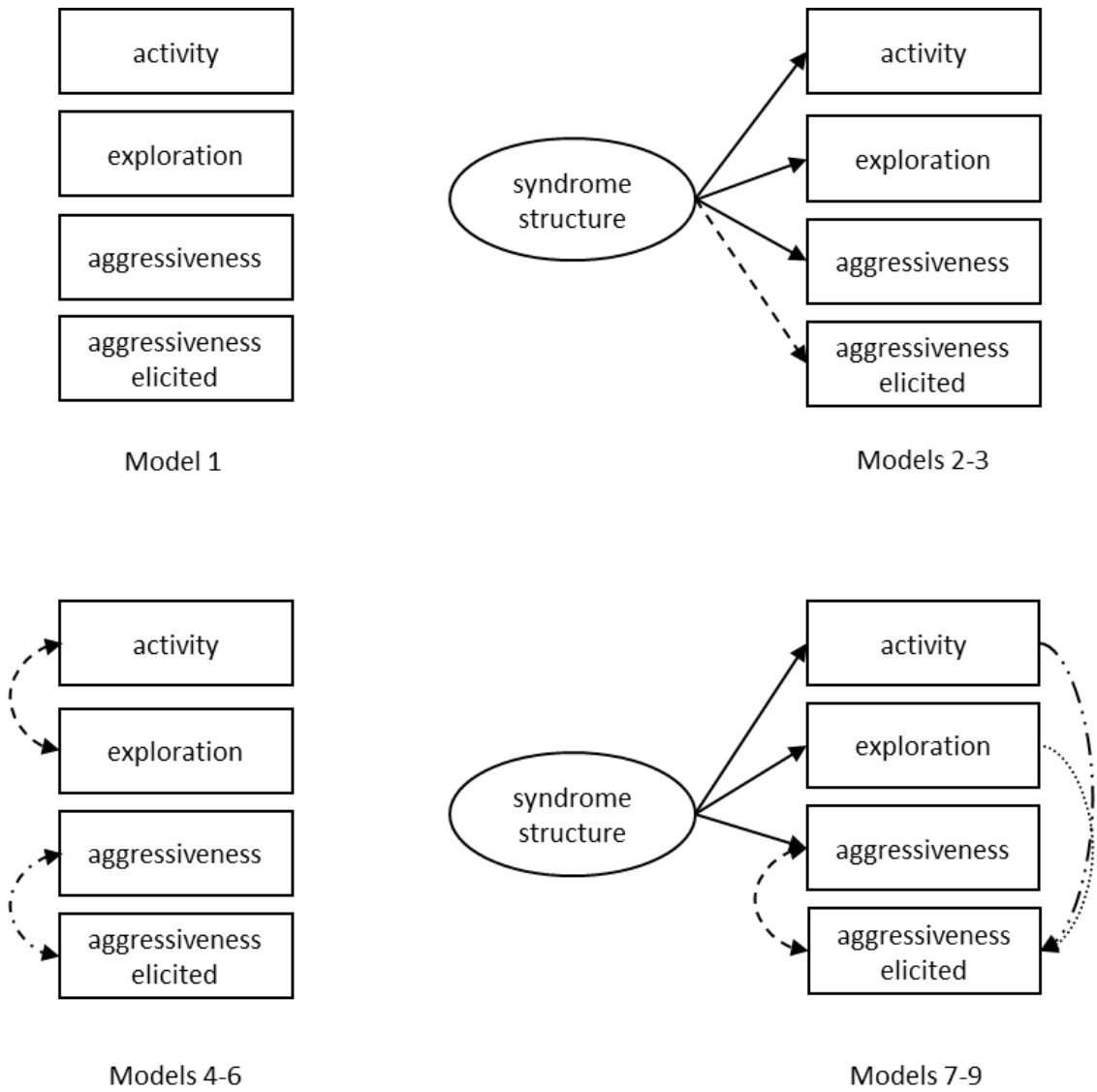


Figure 1.

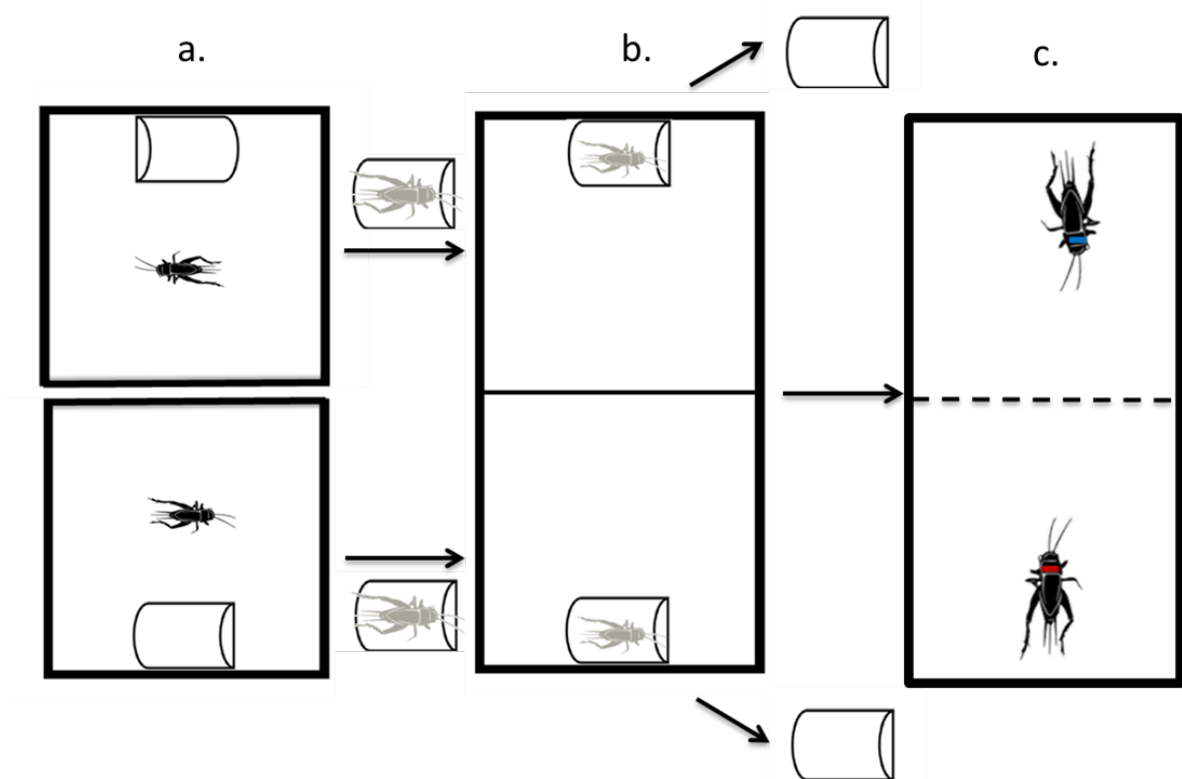


Figure 2.

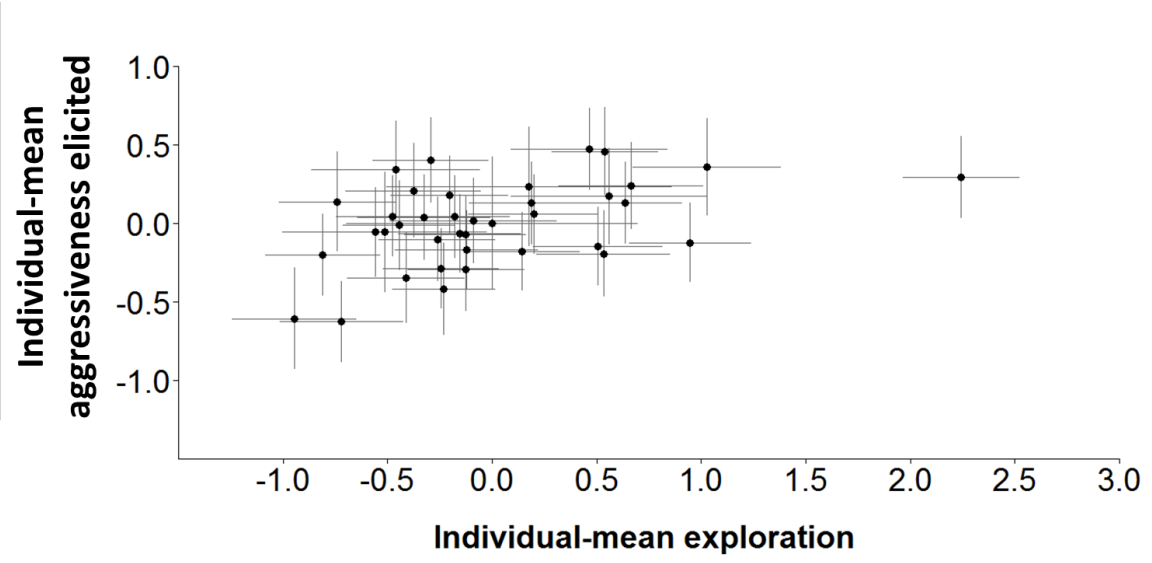


Figure 3.

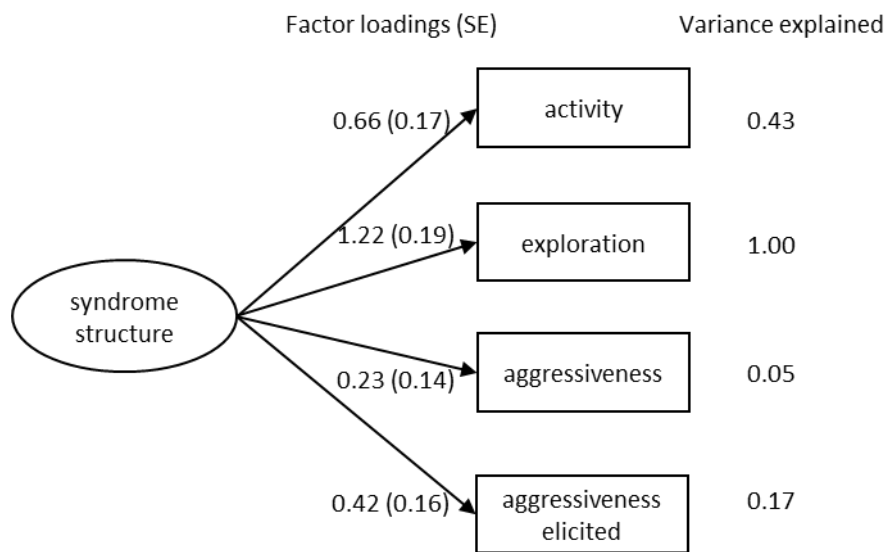


Figure 4.

988 **SUPPLEMENTARY TEXT**

989 As detailed in the main text, analyses of aggressiveness that estimate focal and
990 opponent identity effects typically focus on variation in the behavior expressed by the
991 (arbitrarily assigned) focal individual alone. Here we detail how we incorporated
992 information on the same behavior measured on the opponent in the statistical model
993 while avoiding pseudo-replication. We started with the following data structure, where
994 each line consisted of information regarding the identity of both individuals, one
995 arbitrarily called ‘Individual A’ and the other ‘individual B’, with associated information
996 regarding their aggressiveness:

trial ID	Individual A	Individual B	Aggressiveness A	Aggressiveness B
1	14	12	3	6

997 We then rearranged the data in the following way:

trial ID	Focal	Opponent	Dataset	Aggressiveness 1	Aggressiveness 2
1	14	12	1	3	NA
1	12	14	2	NA	6

998 In this re-ordered dataset, the data is printed over two lines, once viewing individual A
999 as the ‘focal’ individual in trial 1 (Dataset 1) and once viewing individual B as the ‘focal’
1000 individual in trial 1 (Dataset 2). Importantly, the behavior of the individual dubbed

1001 'focal' in Dataset 1 was printed in another column (Aggressiveness 1) than the
1002 behavior of the individual dubbed 'focal' in Dataset 2 (column Aggressiveness 2). We
1003 then proceeded to estimate model parameters under the imposed assumption that all
1004 model parameters (fixed effect coefficients and (co)variance components) are equal
1005 for the homologous traits as defined in the two non-overlapping data sets (i.e.,
1006 Aggressiveness 1, Aggressiveness 2). Practically this can be achieved for a pair of
1007 homologous traits by fitting a bivariate mixed effect model with the following code in
1008 ASReml, which we have annotated in footnotes below:

```
1009 agg1 agg2 ~mu !r !{Trait.foc Trait.opp !}
```

```
1010 1 2 1
```

```
1011 0
```

```
1012 Trait 0 US !GPZP !=a0a !S2==1 #A
```

```
1013 0.5
```

```
1014 0 0.5
```

```
1015 Trait.foc 2
```

```
1016 4 0 US !GPZPUZPZUZP !=a0ab0c0b0c #B
```

```
1017 0.5
```

1018 0 0.5

1019 0.1 0 0.5

1020 0 0.1 0 0.5

1021 foc

1022 The `!{Trait.tag Trait.opp !}` command enables joining the focal and opponent variance-
1023 covariance matrix into a single matrix such that covariances between focal and
1024 opponent identity effects can be estimated.

1025 A – Residual covariance structure. Residual variances are constrained to be positive
1026 and equal for the two traits. A starting value of 0.5 is supplied. Since no line of data is
1027 informative for both traits the residual covariance is not estimable and is fixed
1028 (arbitrarily) to zero.

1029 B – Among-individual covariance structure. There are four random effects in the model
1030 (focal and opponent effects on two homologous traits) so a 4x4 covariance matrix is
1031 specified. Variances are constrained to be positive (starting value of 0.5 supplied for
1032 each), while covariance terms are identifiable between focal and opponent effects
1033 with each trait (starting value of 0.1 supplied). Covariance parameters for Aggression 1
1034 are constrained to equal those of Aggression 2. All other cross-trait covariance terms
1035 are fixed to zero.

1036 **SUPPLEMENTARY TABLES**

1037 **Table S1.** Parameter estimates (with standard errors) of fixed and random effects
1038 derived from our univariate models fitted to analyze variation in activity, exploration,
1039 weight, and aggressiveness (approach, chasing, singing). Values printed in bold face
1040 represent significant effects based either on Wald F tests (fixed effects) or likelihood
1041 ratio tests (random effects) detailed in the main text. Values of adjusted individual and
1042 opponent repeatability reported in Table 2 (main text) are derived from the univariate
1043 models printed here.

	Activity	Exploration	Weight	Approach	Chase	Sing
Fixed effects	β (SE)	β (SE)	β (SE)	β (SE)	β (SE)	β (SE)
Intercept	-0.01 (0.20)	0.16 (0.22)	-0.21 (0.23)	0.33 (0.12)	0.07 (0.10)	0.06 (0.01)
Sequence	-0.03 (0.02)	-0.04 (0.01)	-0.04 (0.01)	-0.07 (0.01)	-0.02 (0.02)	-0.01 (0.02)
Random effects	σ^2 (SE)	σ^2 (SE)	σ^2 (SE)	σ^2 (SE)	σ^2 (SE)	σ^2 (SE)
Focal	0.32 (0.11)	0.40 (0.10)	0.46 (0.11)	0.19 (0.07)	0.09 (0.05)	0.08 (0.05)
Opponent	-	-	-	0.16 (0.07)	0.12 (0.06)	0.05 (0.05)
Group	0.01 (0.07)	0.06 (0.10)	0.15 (0.15)	0.03 (0.09)	0.00 (0.00)	0.00 (0.00)
Date	0.00 (0.02)	0.00 (0.01)	0.18 (0.06)	0.00 (0.03)	0.00 (0.00)	0.04 (0.09)
Residual	0.66 (0.07)	0.55 (0.08)	0.22 (0.04)	0.63 (0.07)	0.78 (0.08)	0.85 (0.09)
Covariance				Cov (SE)	Cov (SE)	Cov (SE)
Focal - Opponent	-	-	-	0.04 (0.05)	-0.03 (0.04)	-0.01 (0.03)

Table S2. Estimated bivariate among-individual correlations for all traits included in our multivariate model (Table 3): activity, exploration, aggression, aggression elicited in others, and body weight. We print here the χ^2 -value (associated degrees of freedom = 1 in all cases) and values of P associated with likelihood ratio tests (LRTs) detailed in the main text (Methods).

Traits	r (SE)	χ^2_1	P
activity - exploration	0.81 (0.08)	18.2	<0.001
activity - aggression	0.39 (0.18)	3.88	<0.05
activity - aggression elicited	0.16 (0.20)	0.63	0.426
exploration - aggression	0.39 (0.17)	230.5	<0.001
exploration - aggression elicited	0.45 (0.17)	5.54	<0.05
aggression - aggression elicited	0.09 (0.22)	0.14	0.700
weight - activity	0.17 (0.15)	225.4	<0.001
weight - exploration	0.22 (0.14)	2.27	0.132
weight - aggression	0.43 (0.16)	5.66	<0.05
weight - aggression elicited	-0.31 (0.18)	2.58	0.110

Table S3. Relative fit of nine candidate models (detailed in the main text) based on the Akaike's information criterion (AIC). We present each model's AIC-value relative to the model with the lowest AIC-value (ΔAIC), its weight, and relative likelihood.

Model	ΔAIC	Akaike Weight	Relative LL
3 - Full domain behavioural syndrome	0	0.75	1
9 – Behavioural syndrome with aggressiveness elicited only affected by exploration	2.35	0.23	0.31
2 - Behavioural syndrome with aggressiveness elicited independent	8.91	0	0.01
8 – Behavioural syndrome with aggressiveness elicited only affected by activity	9.90	0	0
7 – Behavioural syndrome with aggressiveness elicited linked only to aggressiveness	10.78	0	0
4 – General activity syndrome with social behaviours independent	11.62	0	0
6 – Independent social behaviours and general activity syndromes	13.33	0	0
1 – Behavioural independence	48.94	0	0
5 – Social behaviours syndrome with general activity behaviours independent	50.65	0	0

1052 **Table S4.** Estimated among-individual (a) and residual within-individual (b) variances and covariances/correlations (with SE) for two non-
1053 social behaviors (activity and exploration), two social behaviors (aggressiveness and aggressiveness elicited in opponents), and weight.
1054 We present variances on the diagonal, and covariances (correlations) on the lower (upper) off-diagonals, respectively.
1055 Covariances/correlations printed in bold-face are significant based on likelihood ratio tests derived from the multivariate model detailed
1056 in the main text.

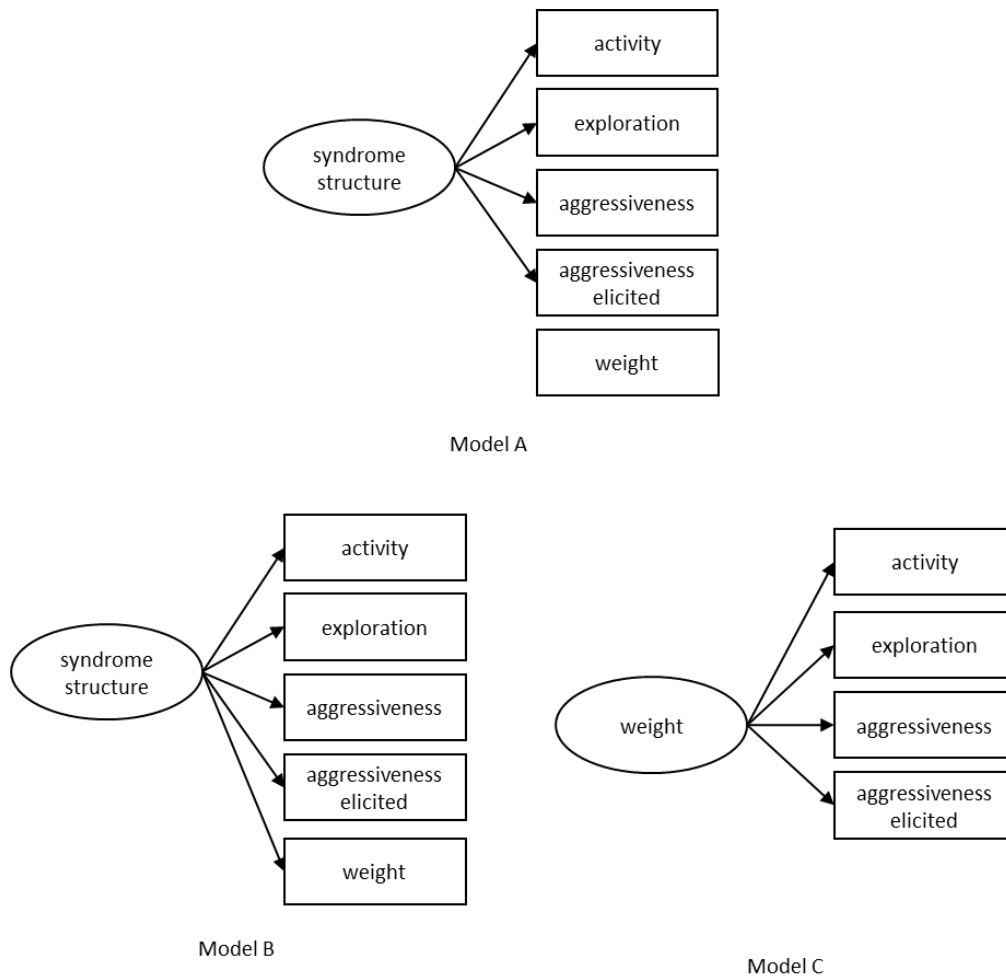
a.	Aggressiveness	Activity	Exploration	Weight	Aggressiveness elicited
Aggressiveness	0.21 (0.07)	0.39 (0.18)	0.39 (0.17)	0.43 (0.16)	0.09 (0.22)
Activity	0.11 (0.06)	0.35 (0.06)	0.81 (0.08)	0.17 (0.15)	0.16 (0.20)
Exploration	0.13 (0.06)	0.33 (0.08)	0.49 (0.10)	0.22 (0.14)	0.45 (0.17)
Weight	0.17 (0.07)	0.08 (0.08)	0.13 (0.09)	0.70 (0.13)	-0.31 (0.18)
Aggressiveness elicited	0.02 (0.04)	0.04 (0.05)	0.13 (0.06)	-0.11 (0.07)	0.18 (0.06)

b.	Aggressiveness	Activity	Exploration	Weight
Aggressiveness	0.61 (0.06)	-0.02 (0.07)	0.03 (0.07)	0.05 (0.06)
Activity	-0.01 (0.04)	0.65 (0.06)	0.17 (0.06)	0.06 (0.06)
Exploration	0.02 (0.04)	0.10 (0.04)	0.52 (0.04)	0.13 (0.06)
Weight	0.03 (0.03)	0.03 (0.03)	0.06 (0.03)	0.35 (0.03)

Table S5. Relative fit of three a posteriori considered models (detailed in the main text) based on the Akaike's information criterion (AIC). We present each model's AIC-value relative to the model with the lowest AIC-value (ΔAIC), its weight, and relative likelihood. Here we investigate how body weight is best incorporated into the best-fitting SEM presented in Table S3. For a visualization of each model's structure, see Fig. S1.

Model	ΔAIC	Akaike Weight	Relative LL
B – Weight as part of the full syndrome	0	0.73	1
A - Weight independent from full domain behavioural syndrome	1.98	0.27	0.37
C – Weight driving the behavioral syndrome	44.93	0	0

SUPPLEMENTARY FIGURES



1065 **Figure S1.** Three a posteriori considered models. The relative fit of these models (Table
 1066 S5) was considered to investigate how body weight is best incorporated into the best-
 1067 fitting SEM presented in Table S3. Model A: weight is independent from the behavioral
 1068 syndrome; model B: weight is part of the syndrome; model C: weight causes the
 1069 behavioral syndrome.

